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## Octomys mimax (Rodentia: Octodontidae)

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Abstract: Octomys mimax O. Thomas, 1920, the viscacha rat, is a surface-dwelling rodent, endemic to the Monte biome of western Argentina. The genus Octomys is monotypic and represents a basal clade within the family Octodontidae. O. mimax is strictly herbivorous and is found in low-elevation arid environments characterized by galleries or rock formations. In these environments, O. mimax nests within rock crevices located inside ravines with relatively low vegetation cover. O. mimax is solitary and mostly nocturnal. Nocturnal activity coupled with a basal metabolic rate and thermal conductance lower than expected for body mass of O. mimax probably represent strategies for water conservation in this species. DOI: 10.1644/853.1.

Key words: Argentine desert rodent, Caviomorpha, Monte ecoregions, rodent, viscacha rat

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## Octomys O. Thomas, 1920

Octomys O. Thomas, 1920:117. Type species Octomys mimax Thomas, 1920, by original designation.

CONTEXT AND CONTENT. Order Rodentia, suborder Hystricomorpha, infraorder Hystricognathi, family Octodontidae. Formerly included 'Octomys' barrerae described later by Lawrence (1941) and transferred to a monotypic genus, Tympanoctomys, by Yepes (1930, 1942). Octomys is monotypic.

## Octomys mimax O. Thomas, 1920 Viscacha Rat

Octomys mimax O. Thomas, 1920:118. Type locality "hilly district known as La Puntilla, near Tinogasta, Catmarca," Argentina (elevation about 1,000 m).

Octomys joannius O. Thomas, 1921:217. Type locality "Pedernal, about 60 km. S. W. of San Juan, and 30 W. of Canada, Honda," (elevation about 1,200 m).

**Fig. 1.**—Adult *Octomys mimax* from Los Rastros area, Parque Natural Provincial Ischigualasto, San Juan Province, western Argentina, trapped below a jarilla shrub (*Zuccagnia punctata*,



Fabaceae); sex not determined. Used with permission of E. Sanabria (photographer).

Octomys mimax mimax: Ellerman, 1940:157. Name combination.

Octomys mimax joannius: Ellerman, 1940:157. Name combination.

CONTEXT AND CONTENT. Context as for genus. *Octomys mimax* is monotypic (Woods and Kilpatrick 2005).

#### **DIAGNOSIS**

Octomys mimax (Fig. 1) resembles other members of family Octodontidae such as the sister taxon Tympanoctomys barrerae (red viscacha-rat) and the closely related Octodontomys gliroides (mountain degu—Contreras et al. 1987). O. mimax is larger in size and has shorter hind feet and tail than T. barrerae (Diaz et al. 2000). Overall coloration of fur is light brown, similar to that of T. barrerae (Diaz et al. 2000).

Distinctive features of the skull of *O. mimax* (Fig. 2) include well-developed tympanic bones, short and rounded nasals, and a short maxillary toothrow (De Santis et al. 1991; Diaz et al. 2000). *O. mimax* has hypertrophied auditory bullae, a characteristic of species living in open and risky habitats. This feature is hypothesized to represent a morphological adaptation to predator avoidance due to specialized acoustic sense for low-frequency sounds (Diaz et al. 2000; Köhler et al. 2000; Mares et al. 2000; Ojeda et al. 1999; Ojeda and Tabeni 2009; Olivares et al. 2004; Verzi 2001; Verzi and Quintana 2005). Compared to other octodontids, the tympanic bullae of *O. mimax* are the 2nd largest after *T. barrerae* (Gallardo et al. 2007; Novak 1999; Redford and Eisenberg 1992).

#### **GENERAL CHARACTERS**

Octomys mimax is a medium-sized rodent that exhibits no sexual dimorphism in body mass. Body masses for O. mimax were recorded by 2 of us (R. Sobrero and V. E. Campos). Mean body mass was 102.8 g  $\pm$  18.2 SD for 14 livetrapped specimens (6 adult males and 8 adult females) from Parque Provincial Ischigualasto (San Juan Province, Argentina). Mean body mass was 95.8 g  $\pm$  20.1 SD for 12 preserved specimens (6 adult males and 6 adult females) from Parque Provincial Ischigualasto and 120 g for an additional adult specimen (sex unknown) from Cañón del Talampaya, Parque Nacional Talampaya (La Rioja Province, Argentina). External measurements (mean  $\pm SD$ , mm) based on 13 adult males and 16 adult females from Parque Provincial Ischigualasto were: total length,  $279.3 \pm 51.7$ ; length of head and body,  $133.9 \pm 44.6$ ; length of tail, 145.4 $\pm$  25.6; length of hind foot, 35.40  $\pm$  1.5; and length of ear,  $21.8 \pm 2.2$ .

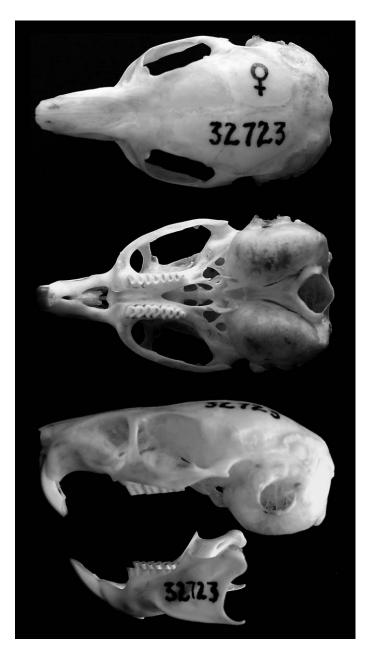


Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult female *Octomys mimax* (specimen MZUC-UCCC [Museo de Zoología Universidad de Concepción—Universidad de Concepción Colecciones Científicas] 32723) from Los Rastros area, captured in Parque Provincial Ischigualasto, San Juan Province, Argentina.

Ears are relatively hairless and have guard hairs in front of the meatus (Redford and Eisenberg 1992). Dorsal pelage is light brown; the underparts and front and hind feet are white (Novak 1999; Redford and Eisenberg 1992). The bushy tail is short, well haired to the tip, and bicolored, with a conspicuous terminal tuft making up about 50% of its total length (Redford and Eisenberg 1992). The tarsi are long and

sturdy; both front and hind feet have 5 digits (Cabrera and Yepes 1940; Orlog and Lucero 1981; Redford and Eisenberg 1992).

Standard craniodental features for O. mimax were assesed by 2 of us (R. Sobrero and V. E. Campos). Cranial measurements (mean  $\pm$  SD, mm) based on 13 adult specimens (6 males, 6 females, and 1 unknown sex) were: length of rostrum,  $19.1 \pm 2.4$  (n = 13); length of diastema,  $8.9 \pm 1.2$  (n = 13); basicranial length (lengths of basioccipital + basisphenoid),  $17.1 \pm 2.8$  (n = 13); length of tympanic bullae,  $14.3 \pm 1.1$  (n = 13); length of masseter out-lever arm, 25.9  $\pm$  3.0 (n = 13); height of mandibular condyle,  $5.3 \pm 1.3$  (n = 13); mandibular width,  $18.4 \pm 1.7$  (n = 13); = 12); upper incisor width,  $3.4 \pm 0.6$  (n = 13); and length of zygomatic arch,  $17.6 \pm 1.8$  (n = 13). Other cranial measurements (mean  $\pm$  SD, mm) for 12 adult specimens (6 males, 5 females, and 1 sex unknown) were: width of zygomatic arch,  $19.6 \pm 1.5$  (n = 12); condylobasal length,  $20.5 \pm 2.3$  (n = 12); least interorbital breadth,  $5.9 \pm 0.5$  (n = 12); least interpretain breadth,  $5.0 \pm 0.5$  (n = 12); least interpretain breadth,  $5.0 \pm 0.5$  (n = 12); least interpretain breadth,  $5.0 \pm 0.5$  (n = 12); least interpretain breadth,  $5.0 \pm 0.5$  (n12); length of maxillary toothrow,  $8.0 \pm 0.9$  (n = 12); length of mandibular toothrow,  $8.2 \pm 1.0$  (n = 12); and bullar width,  $7.6 \pm 0.5$  (n = 12). For 5 adult specimens bullar index and lower incisor index were both 0.3 (Ojeda et al. 1999).

We (R. Sobrero and V. E. Campos) also measured 2 juveniles. Measurements (mm) for a juvenile male with no scrotal testes were: length of head and body, 130.0; length of tail, 145.0; length of hind foot, 30.0; length of ear, 15.0; and body mass, 71 g. For a juvenile female with closed vagina, measurements (mm) were: total length, 115.0; length of tail, 155.0; length of hind foot, 30.0; length of ear, 15.0; and body mass, 71 g.

### **DISTRIBUTION**

Octomys mimax is endemic to western Argentina, inhabiting lowland deserts with abundant rocks, rocky desert foothills, low scrub areas, ravines, and gorges at elevations ≤ 800 m (Fig. 3; Blair et al. 1976; J. K. Braun, pers. comm.; Contreras et al. 1987; Gallardo et al. 2007; Mares 1975; Mares and Ojeda 1982; Novak 1999; Orlog and Lucero 1981). Today, the species is distributed in the temperate Monte Desert and areas of the northern monte in mountains and basins of Catamarca, San Juan, La Rioja, and San Luis provinces of Argentina (Fig. 3; J. K. Braun, pers. comm.; Ebensperger et al. 2008; R. A. Ojeda, pers. comm.; Olivares et al. 2004; Oyarce 2005). It is thought that formerly the distribution of O. mimax extended south into northern Mendoza Province (Fig. 3; Barquez et al. 2006; Cabrera 1958, 1961; Gallardo et al. 2007; Honacki et al. 1982; Mares 1973; Mares and Ojeda 1982; Ojeda and Tabeni 2009; R. A. Ojeda, pers. comm.; Redford and Eisenberg 1992; Reig 1986; Verzi 2001).

Octomys mimax is known from 5 localities in San Juan Province: Pedernal, Sarmiento; Río de los Patos, Valle Calingasta; a site near the divergence of the Bermejo and

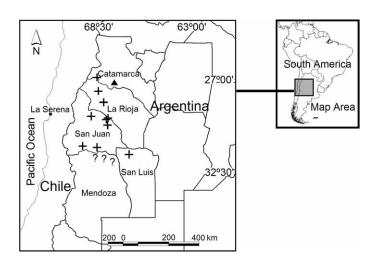


Fig. 3.—Geographic distribution of *Octomys mimax*. Solid triangle indicates type locality in La Puntilla area, Catamarca Province, Argentina. Cross symbols indicate localities where *O. mimax* has been recorded in Monte Desert of La Rioja, San Juan, and San Luis provinces (J. K. Braun, pers. comm.; Diaz and Ojeda 1999; Ebensperger et al. 2008; Gallardo and Kirsch 2001; Honeycutt et al. 2003; Köhler et al. 2000; R. A. Ojeda, pers. comm.; Olivares et al. 2004; Oyarce 2005; Redford and Eisenberg 1992). Question marks indicate regions that species may inhabit (e.g., Barquez et al. 2006; Cabrera 1958, 1961; Honacki et al. 1982; Mares 1973; Mares and Ojeda 1982; R. A. Ojeda, pers. comm.; Redford and Eisenberg 1992; Reig 1986; Verzi 2001). Map redrawn with modifications from Redford and Eisenberg (1992) with permission.

Jáchal rivers, Valle del Rio Bermejo; Valle San Agustín, Sierra del Valle Fértil; and 2 areas of the Parque Provincial Ischigualasto: Los Rastros and El Gusano (Fig. 3; J. K. Braun, pers. comm.; Diaz and Ojeda 1999; Ebensperger et al. 2008; Gallardo and Kirsch 2001; Honeycutt et al. 2003; Köhler et al. 2000; R. A. Ojeda, pers. comm.; Olivares et al. 2004; Oyarce 2005; Redford and Eisenberg 1992). The species is also found in 4 or 5 localities in La Rioja Province: near Cañón de Talampaya, Parque Nacional Talampaya; possibly in Villa Unión; and in 3 other sites along the riverbed of Río Bermejo that runs in a northwest-easterly direction (Fig. 3; Honeycutt et al. 2003; R. A. Ojeda, pers. comm.; Redford and Eisenberg 1992). The capture of 2 females (854 m elevation) in western Hualtaran, Parque Nacional Sierra de las Quijadas, confirms the presence of O. mimax in San Luis Province (J. K. Braun, pers. comm.; R. A. Ojeda, pers. comm.). No fossils of *O. mimax* are known (D. H. Verzi, pers. comm.).

## FORM AND FUNCTION

Form.—Dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20; cheek teeth have a simplified occlusal pattern in a figure-eight shape (De Santis et al. 1991; Redford and Eisenberg 1992). The relationship between craniodental features and

modes of chewing in this family of rodents is complex (De Santis et al. 1998; De Santis and Moreira 2000; Vassallo and Verzi 2001). This relationship allows us to infer the development of the chewing muscles, feeding, and digging with the teeth (e.g., De Santis and Moreira 2000; Olivares et al. 2004). Octomys mimax exhibits propalinal and bilateral grinding (Olivares et al. 2004; Vassallo and Verzi 2001; Verzi 2001; Wilkins and Cunningham 1993), 2 features that may have evolved independently at least twice in the O. mimax + T. barrerae clade (Olivares et al. 2004; Verzi 2001). The observation of tooth scars in rodents allows determination of the prevailing direction of masticatory movements (e.g., Wilkins and Cunningham 1993). The orientation (angle) of tooth scars (striations) present on the enamel of O. mimax is < 10°, a feature associated with posteroanterior jaw displacement and simultaneous occlusion (Olivares et al. 2004). The relationship between upper and lower molars in functional contact during activity of the mandible (occlusion) is nearly horizontal (Olivares et al. 2004). A simplified pattern of enamel bands characterizes the occlusal design of molars (Reig 1970; Verzi 2001). The reentrant folds of the upper molars in O. mimax meet in the middle of the teeth (Novak 1999).

There is a dense concentration of vibrissae in the oral cavity, along the midline of the palate just caudal to the incisors (Berman 2003). Vibrissae are about 3 mm long and are in contact with the facial muscle bucccinatorius pars intermaxillaris (Berman 2003). The closely related species *T. barrerae* has specialized oral vibrissae that are used to strip salt-laden epidermis from leaves of halophytes that the species eats, but function of vibrissae in *O. mimax* is not known, because the species does not eat halophytes (Berman 2003). Berman (2003) suggests that in *O. mimax* vibrissae may have a tactile function and sense the position of food in the oral cavity.

The jugal process of *O. mimax* is variable, and the lacrimal does not open on the side of the rostrum; the paraoccipital process is short and the dentary is very pronounced (Redford and Eisenberg 1992). Maximum diameter of erythrocytes is 6.9 µm (Gallardo et al. 2003).

Morphology of the glans penis of O. mimax is similar to that of other South American hystricognaths (Contreras et al. 1993; Spotorno 1979). The baculum (os penis) is positioned dorsally; the intromittent sac, an invagination of the distal part of the glans, lies below the urethra and is everted during sexual activity (Contreras et al. 1993). There are penial spikes on the surface of the glans and the sac, which point backward during erection (Contreras et al. 1993; Spotorno 1979). Mean spike length is 3.4 mm; baculum is elongated and tapering to a tip with mean length of 9.0 mm; mean width is 1.5 mm; and mean robustness index (maximum width  $\div$  length) is 0.17 (n = 7—Contreras et al. 1993). The elongation of the glans penis, indicated by an elongation of the baculum, may be related to the constancy in the pattern of spikes (Contreras et al. 1993).

The spikes and general penial morphology have been used as a phylogenetic signal in octodontids, and they confirm the close relationship between O. mimax and T. barrerae and their difference from other octodontids (Contreras et al. 1993; Gallardo et al. 2004; Spotorno 1979). Of 9 octodontid species studied, most species had 2 spikes on each side of the intromittent sac (the "2–2" pattern), but only O. mimax and T. barrerae consistently had 1 spike on each side ("1–1" pattern; n=7 in each species—Contreras et al. 1993). Contreras et al. (1993) suggested that the 1–1 pattern is ancestral to the 2–2 pattern in living Octodontidae.

Function.—Basal metabolic rate and thermal conductance of Octomys mimax are slightly less than expected for body mass (Bozinovic and Contreras 1990). For 8 individuals (4 males and 4 females) with a mean body mass of 118.6 g, mean basal metabolic rate, in milliliters of O<sub>2</sub>, was  $0.97 \text{ ml g}^{-1} \text{ h}^{-1} \pm 0.11 \text{ SD}$ . Body temperature is maintained at 36.7°C ± 0.6°C in individuals exposed to ambient temperatures of 5-35°C, indicating that the species thermoregulates well and can maintain a high body temperature even during cold nights (Bozinovic and Contreras 1990). The lower limit of the thermoneutral zone is 22.2°C. Mean thermal conductance (an inverse measure of insulation) for the same 8 individuals, in milliliters of  $O_2$ , was 0.07 ml  $g^{-1} h^{-1}$ °C<sup>-1</sup>, lower than expected for body weight, indicating that O. mimax is relatively well insulated for its size (Bozinovic and Contreras 1990).

Kidneys of O. mimax show no evidence of specialization for arid habitat; they are not specialized for water conservation, as are kidneys in many desert rodents that produce highly concentrated urine. Mean urine concentration of O. mimax from the field was 2,071 mOsm/l (n = 11individuals), much less concentrated than found in other desert rodents, including the sister taxon Tympanoctomys barrerae (Diaz and Ojeda 1999). Mean kidney mass was  $0.52 \text{ g} \pm 0.14 \text{ SD}$  (n = 9—Diaz 2001; Diaz et al. 2006), the medulla is composed of 2 zones, and the single short papilla does not extend into the ureter (Diaz and Ojeda 1999). Relative medullary thickness, a measure of kidney morphology, is determined by calculating the ratio of 10 times the medullary thickness to the cube root of the product of length × width × thickness of the kidney. In O. mimax relative medullary thickness is  $6.09 \pm 0.06$  SE (n = 11 individuals), considerably lower than the value for other desert rodents (Diaz and Ojeda 1999). Other kidney dimensions measured on the same 11 O. mimax from Parque Provincial Ischigualasto by Diaz and Ojeda (1999) were cortex thickness, 1.74 mm  $\pm$  0.02 SE, and medullary thickness,  $6.38 \pm 0.08$  mm. Two additional indices measured on the same specimens also were low compared to other desert rodents: ratio of inner medulla to cortex,  $2.58 \pm 0.03$  SE, and relative medullary area (ratio of medullary area to cortical area),  $0.83 \pm 0.01$  SE (n = 6; Diaz and Ojeda 1999).

#### **ECOLOGY**

Octomys mimax is distributed in the temperate Monte Desert in Catamarca, San Juan, La Rioja, and perhaps in Mendoza provinces. In San Luis Province, O. mimax occurs in a transition area between the Monte and Chaco Seco (M. A. Mares and J. K. Braun, pers. comm.). The Chaco Seco is 1 of the 5 subregions of the semidesert Chaco Arido biome, the most common biome in Argentina (Burkart et al. 1999).

The Monte extends over about 2,000 km, from 24°S to 43°S latitude, occupying a northwest-southeast-oriented strip of land (Morello 1958). Thus, the Monte Desert is a biome with different climate and edaphic conditions throughout its expanse. This biome is divided into 2 subregions or ecoregions, the northern Monte of mountains and closed basins (Monte de Sierras y Bolsones) between 24°S and 32°S latitude, and the southern Monte of plains and plateaus (Monte de Llanuras y Mesetas) between 32°S and 37°S (Burkart et al. 1999). Precipitation along this gradient ranges from seasonal summer rains of 83–293 mm in the north to the absence of a well-defined rainy season, 89–187 mm, in the south (Mares et al. 1985). Maximum average temperature in the Monte ranges from 27.0°C in the north (Tinogasta, Catamarca Province) to 20.4°C in the south (Trelew, Chubut Province), whereas minimum temperature ranges between 7.5°C and 7.3°C at the same localities (Cabrera 1976). In the central portion of the Monte, in Mendoza Province, average annual precipitation is about 326 mm, with marked seasonality of humid summers and dry winters (Ojeda et al. 1998). At the transition between the Monte and Chaco Seco biomes, in San Luis Province, climate conditions are more humid, with annual precipitation reaching nearly 400 mm, concentrated mostly in summer (Burkart et al. 1999).

The Monte has a diverse mosaic of habitats and plant associations. Xerophytic hillsides with bromeliads (*Deutherocohnia* and *Tillandsia*) and cacti (*Trichocereus*); forests and woodlands of *Prosopis* mixed with grasses; shrublands dominated by evergreen zygophyllaceous shrubs such as *Larrea*, *Bulnesia*, and saltbush (*Atriplex*); salt flats (salares) surrounded by rings of halophytic vegetation; sand dunes; bare muddy depressions (barreales); and badlands make up most of the heterogeneous landscapes of the Monte (Morello 1958). The Chaco Seco, a semiarid biome, is richer than the Monte in floristic elements, and new or different plant species occur there, such as *Aspidorpema*, *Acacia*, *Jatropha*, and *Mimoziganthus*, among others (Burkart et al. 1999).

Information on the ecology of *O. mimax* is scarce, but its distribution seems restricted to areas with rocky slopes and ravines (Gallardo et al. 2007; Mares 1980; Ojeda et al. 1996). *O. mimax* of Parque Provincial Ischigualasto is so far the most studied population and occurs in the most arid portion of the Monte Desert. This region corresponds to the Monte de Sierras y Bolsones, the climate is very arid with summer rains < 100 mm per year (concentrated in

November–February), and absolute minimum temperature in winter is  $-10^{\circ}$ C and absolute maximum in summer is  $45^{\circ}$ C (Campos et al. 2008). Hard substrates predominate, fundamentally Triassic sandstones of variable salt content, cut by abrupt gullies that drain water during rainy periods. There are also fine-textured substrates (sands and clays) in which the vegetation is drawn to areas where water accumulates after rainfall. The predominant habitat is open scrubland (Márquez 1999), and vegetation includes the shrubs *Larrea cuneifolia*, *Zuccagnia punctata*, and *Deuterocohnia longipetala* and cacti, including *Opuntia sulphurea*, *Denmoza rhodacantha*, and *Trichocereus strigosus*. Columnar cacti (*Trichocereus terscheckii*) occupy stony hillsides (Burkart et al. 1999). Overall plant coverage is nearly 15% (Márquez et al. 2005).

The rocky habitat used by *O. mimax* in Parque Provincial Ischigualasto is clumped, and is characterized by relatively low plant cover (19.1%  $\pm$  6.7% SE) and high percentage of bare substrate (80.9%  $\pm$  6.7%). The bare ground of sites used by *O. mimax* is composed of soil (39.1%  $\pm$  6.1%) and rocks (41.9%  $\pm$  8.5%). The mean ( $\pm$  SE) height of vegetation at these sites is 83.2  $\pm$  8.9 cm (Ebensperger et al. 2008). The plant species *Prosopis torquata* ( $\bar{X} = 1.01 \pm 0.42$  SD; U = 187.00, d.f. = 1, P = 0.545) and *Larrea cuneifolia* ( $\bar{X} = 0.65 \pm 0.26$  SD; U = 165.00, d.f. = 1, P = 0.207) are dominant at sites with evidence of activity of *O. mimax*. According to studies carried out by Ebensperger et al. (2008), both sexes rest individually in places with similar amounts of plant cover, rocks, and soil characteristics.

Male and female *O. mimax* live solitarily, which fits the general pattern of social behavior among species of desert habitats (Ebensperger et al. 2008). A study in which 7 *O. mimax* (4 females and 3 males) were tracked with radiotelemetry over a period of 6 days showed that adult males and females do not share resting sites during the day (Ebensperger et al. 2008). *O. mimax* has relatively large home ranges (12,370 m<sup>2</sup>  $\pm$  2,975 *SE*, n = 7) and low to moderate spatial overlap with neighbors, implying that neighbors may occasionally interact socially (Ebensperger et al. 2008). Males of *O. mimax* exhibit larger range areas than females, although spatial overlap among conspecifics is similar for the 2 sexes (Ebensperger et al. 2008).

Rocky habitats are very complex environments, providing crevices and ravines where animals can build nests, seek shelter, and find shade (e.g., George 1986; Mares and Lacher 1987; Nutt 2005; Trainor et al. 2000). The use of rocky habitat may benefit *O. mimax* through providing a thermally stable environment. Two of us (V. E. Campos and S. M. Giannoni) observed the stabilizing effect that rocky habitats have on temperature. For instance, we recorded maximum temperature of the soil measured inside rocky outcrops used as nesting places or refuges by *O. mimax* as  $28.3^{\circ}\text{C} \pm 5.0 \text{ SD}$  when outside temperature was  $43.4^{\circ}\text{C} \pm 9.8^{\circ}\text{C}$ . We also noted that air temperature was more moderate inside rocky

outcrops (maximum air temperature =  $28.3^{\circ}$ C  $\pm 4.3^{\circ}$ C, n = 2) compared to outside ( $32.8^{\circ}$ C  $\pm 7.1^{\circ}$ C, n = 2).

In addition to the temperature-moderating effect provided by the rocky habitat, activity could allow *O. mimax* to avoid the high temperatures and low relative humidity of the day. *O. mimax* has been presumed to be nocturnal (Bozinovic and Contreras 1990; Mares and Ojeda 1982), and recent radiotelemetry studies support this pattern (Ebensperger et al. 2008). Nocturnal activity would allow *O. mimax* to avoid high temperatures and low relative humidity of the day (Bozinovic and Contreras 1990). This hypothesis is supported by the observation that in the habitat where *O. mimax* occurs, air temperature measured 10 cm aboveground in spring during the day was nearly twice that in the night (day:  $\bar{X} = 19.6^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$  *SE*, n = 11; night:  $9.4^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$ , n = 11—V. E. Campos and S. M. Giannoni, in litt.).

Our unpublished observations indicate that the occurrence of *O. mimax* is associated with the presence of large rocks ( $\leq$ 150 cm) and that the species uses rock crevices for nesting. Crevices used were (mean  $\pm$  *SD*) 35.3  $\pm$  2.3 cm high, 20.2  $\pm$  1.9 cm deep, and 174.5  $\pm$  8.0 cm wide.

There is no evidence that *O. mimax* modifies its nesting site either through digging or forming mounds of fresh dirt or rocks (Ebensperger et al. 2008). However, *O. mimax* may modify nests by carrying pieces of cactus to the nest and placing them at tunnel entrances, presumably to make it more difficult for predators to enter (Mares 1976).

Betancourt and Saavedra (2002) suggested that *O. mimax* produces middens, providing important sources of paleontological evidence similar to the genus *Neotoma* (e.g., Wells 1976). Two of us (V. E. Campos and S. M. Giannoni) have located middens at Parque Provincial Ischigualasto. Middens are among the crevices formed between rocks, near nests of *O. mimax*, where there is clear evidence of the presence of this species, such as fresh feces and footprints. Although we have no idea how old are these middens, they seem to be active.

Octomys mimax is strictly herbivorous (Berman 2003; Mares 1973; Mares et al. 1997; Ojeda et al. 1999; Ojeda and Tabeni 2009; Orlog and Lucero 1981; Oyarce 2005; Redford and Eisenberg 1992). Main food items consumed include leaves, fruits, seeds, and pods (Oyarce 2005). This species does not remove epidermis from leaves (e.g., it is not a leaf shaver) as does Tympanoctomys barrerae, which feeds on halophytes (Giannoni et al. 2000; Mares et al. 1997; Ojeda et al. 1999). Although O. mimax is not specialized for consuming Cactaceae, it does feed on them (Oyarce 2005). Observations at Parque Provincial Ischigualasto indicate that the percentage of cacti consumed is relatively low (29%) during the wet season (Oyarce 2005; M. L. Reus, in litt.), but higher (57%) during dry seasons (M. L. Reus, in litt.). The species also consumes Chenopodiaceae during the dry season in similar proportions to cacti (Oyarce 2005). Foliage of Prosopis (Fabaceae) represents 50-100% of food consumed during the dry season (Oyarce 2005). Consumption of foliage decreases to 20% during the wet season when animals consume relatively more propagules of Prosopis (Oyarce 2005). Maytenus viscifolia (Celastraceae) represents another 20% of the diet during the wet season (Ovarce 2005). Other plants consumed during the dry season include Capparis atamisquea (Capparidaceae) and Cressa nudicaulis (Convolvulaceae). Relatively low amounts of fruits of Lycium (Solanaceae) and leaves of Larrea cuneifolia (Zigofilaceae) are taken during both seasons (Oyarce 2005). Although kidneys of O. mimax have no morphophysiological specialization to arid habitats (Diaz 2001; Diaz and Ojeda 1999), this species could obtain both preformed and metabolic water from its food. O. mimax consumes a great variety of plant parts, including cacti, leaves, pods of Prosopis, and drupe-type fruits (e.g., Lycium) from which these animals may obtain preformed water. The diet also includes seeds rich in carbohydrates (e.g., Prosopis), a potential source of metabolic water. Indeed, observations by one of us (V. E. Campos) suggest that O. mimax obtains seeds of Prosopis from the feces of donkeys (Equus asinus) and maras (Dolichotis patagonum).

No information has been reported on density fluctuations of populations of *O. mimax*. Qualitative information indicates that abundance is generally low (Ebensperger et al. 2008), but data on population sizes from year to year would be valuable, because interyear variation tends to characterize other desert rodent populations (e.g., Randall et al. 2005).

### **GENETICS**

Octomys mimax has a diploid number (2n) of 56 chromosomes, and a fundamental number (FN) of 108. Heterochromatin is restricted to the pericentric regions in all chromosomes, with the exception of chromosome number 27 and the X chromosome (see Contreras et al. 1994). The karyotype is composed of 5 small submetacentric chromosomes, 21 small metacentric chromosomes, and 1 small subtelocentric chromosome. The X and Y chromosomes are a small subtelocentric and a medium-sized metacentric, respectively (Contreras et al. 1994). Analyses of somatic tissues through flow cytometry indicate that O. mimax has a genome of 8.0 picograms of DNA (Gallardo et al. 1999). The gametic genome (of the sperm) was estimated at 4.1 picograms of DNA (Gallardo et al. 2003, 2004).

Based on allozyme phylogenetic analyses the sister species of *O. mimax* is *Tympanoctomys barrerae*, a relation that is highly supported with bootstrap analysis (Gallardo 1997; Köhler et al. 2000). Furthermore, these results are also supported by DNA-DNA hybridization (Gallardo and Kirsch 2001) and karyotypic data (Gallardo 1997; Gallardo et al. 2004; Köhler et al. 2000). A high overall DNA similarity and shared band homology support the hypothesis

of interspecific genomic hybridization between these taxa (Gallardo et al. 2004).

Ancestral forms of *Octomys* have been hypothesized to play major roles during the evolution of the O. mimax + (T.barrerae + Pipanacoctomys aureus [golden viscacha-rat]) clade. In particular, 2 Octomys species may have given rise to P. aureus (which is tetraploid, 4n = 92—Gallardo et al. 2007). The karvotypic model of evolution for the clade containing O. mimax, T. barrerae, and P. aureus is based on matching chromosome number (Gallardo et al. 2007). Assuming that the ancestral lineage to O. mimax produced unreduced, 56-chromosome gametes, its hybridization to P. aureus (producing 46-chromosome gametes) is claimed to have resulted in the 102-chromosome karyotype of T. barrerae (Gallardo et al. 2007). Although the intrinsic mechanisms that caused these speciation events are poorly known, factors such as the origin of South American deserts likely played a role (Gallardo and Kirsch 2001; Opazo 2005).

## **CONSERVATION**

Although the International Union for the Conservation of Nature and Natural Resources considers *Octomys mimax* to have a low risk of extinction (Least Concern—International Union for Conservation of Nature and Natural Resources 2009), updated information on the status of populations of *O. mimax* is strongly needed. In addition to the Least Concern categorization, Reca et al. (1996) considered the species as not threatened. Recently, however, *O. mimax* has been categorized as a mammal of special attention at the Parque Provincial Ischigualasto (Acosta and Murúa 1999). Additionally, the Secretaría de Agricultura, Ganadería, Pesca y Alimentos (Ministerio de Economía y Producción, Government of Argentina) by resolution 144/83 included the species as vulnerable in the *Red Book* of threatened mammals of Argentina (Barquez et al. 2006; Diaz and Ojeda 2000; Ojeda and Diaz 1997).

## **REMARKS**

Octomys mimax has been reported to be rare and difficult to trap (Novak 1999). However, in Parque Provincial Ischigualasto, individuals of this species were successfully captured inside ravines and rock crevices using locally produced metal live traps of medium (28 by 9 by 8 cm) and large (30 by 10 by 9.5 cm) sizes (similar to Sherman traps [H. B. Sherman Traps, Inc., Tallahassee, Florida]—Ebensperger et al. 2008). Traps were distributed equally by size and total number between ravines and baited with a mix of rolled oats and tuna (Ebensperger et al. 2008).

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### LITERATURE CITED

- Acosta, J. C., and F. Murúa. 1999. Lista preliminar y estado de conservación de la mastofauna del Parque Natural Ischigualasto, San Juan, Argentina. Multequina 8:121–129.
- Barquez, R. M., M. M. Diaz, and R. A. Ojeda (eds). 2006. Mamíferos de Argentina: sistemática y distribución. Sociedad Argentina para el Estudio de los Mamíferos, Tucumán, Argentina.
- Berman, S. L. 2003. A desert octodontid rodent, *Tympanoctomys barrerae*, uses modified hairs for stripping epidermal tissue from leaves of halophytic plants. Journal of Morphology 257:53–61.
- Betancourt, J. L., and B. Saavedra. 2002. Paleomadrigueras de roedores, un nuevo método para el estudio del Cuaternario en zonas áridas de Sudamérica. Revista Chilena de Historia Natural 75:527–546.
- BLAIR, W. F., A. C. HULSE, AND M. A. MARES. 1976. Origins and affinities of vertebrates of the North American Sonoran Desert and the Monte Desert of northwestern Argentina. Journal of Biogeography 3:1–18.
- BOZINOVIC, F., AND L. C. CONTRERAS. 1990. Basal rate of metabolism and temperature regulation of two desert herbivorous octodontid rodents: *Octomys mimax* and *Tympanoctomys barrerae*. Oecologia 84:567–570.
- Burkart, R., N. O. Bárbaro, R. O. Sánchez, and D. A. Gómez. 1999. Ecoregiones de la Argentina. Administración de Parques Nacionales, Buenos Aires, Argentina.
- CABRERA, A. 1958. Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencia Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales, Ciencias Zoológicas 4:1–308. [Dated 1957; published 27 March 1958, see notice on p. 308.]
- Cabrera, A. 1961. Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencia Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales, Ciencias Zoológicas 6:161–247.
- Cabrera, A. 1976. Regiones fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura y Jardinería. Tomo 2. ACME, Buenos Aires, Argentina.

- Cabrera, A., and J. Yepes. 1940. Mamíferos Sudamericanos (vida, costumbre, descripción). Historia Natural Ediar. Compañía Argentina de Editores, Buenos Aires, Argentina.
- CAMPOS, C. M., B. PECO, V. E. CAMPOS, J. E. MALO, S. M. GIANNONI, AND F. SUÁREZ. 2008. Endozoochory by native and exotic herbivores in dry areas: consequences for germination and survival of *Prosopis* seeds. Seed Science Research 18:91–100.
- Contreras, L. C., J. C. Torres-Mura, A. E. Spotorno, and F. M. Catzeflis. 1993. Morphological variation of the glans penis of South American octodontid and abrocomid rodents. Journal of Mammalogy 74:926–935.
- CONTRERAS, L. C., J. C. TORRES-MURA, A. E. SPOTORNO, AND L. I. WALTER. 1994. Chromosomes of Octomys mimax and Octodontomys gliroides and relationships of octodontid rodents. Journal of Mammalogy 75:768–774.
- Contreras, L. C., J. C. Torres-Mura, and J. L. Yáñez. 1987. Biogeography of octodontid rodents: an eco-evolutionary hypothesis. Fieldiana: Zoology 39:401–411.
- De Santis, L. J. M., and G. J. Moreira. 2000. El aparato masticador del género extinto *Actenomys* Burmeister, 1888 (Rodentia, Ctenomyidae): inferencias sobre su modo de vida. Estudios Geológicos 56:63–72.
- De Santis, L. J. M., G. J. Moreira, and E. R. Justo. 1998. Anatomía de la musculatura branquiomérica de algunas especies de *Ctenomys* Blainville, 1826 (Rodentia, Ctenomyidae): caracteres adaptativos. Boletín de la Sociedad de Biología de Concepción 69: 89–107.
- DE SANTIS, L., V. ROIG, AND E. R. JUSTO. 1991. La anatomía craneodentaria de *Tympanoctomys barrerae* (Lawrence): comparación con *Octomys mimax* y consideraciones acerca de su estado taxonómico (Rodentia: Octodontidae). Neotropica 37:113–122.
- DIAZ, G. B. 2001. Ecofisiología de pequeños mamíferos de las Tierras Áridas de Argentina: adaptaciones renales. Ph.D. dissertation, Universidad Nacional de Cuyo, Mendoza, Argentina.
- DIAZ, G. B., AND R. A. OJEDA. 1999. Kidney structure and allometry of Argentine desert rodents. Journal of Arid Environments 41: 453-461
- DIAZ, G. B., AND R. A. OJEDA (EDS). 2000. Libro rojo de mamíferos amenazados de Argentina. Sociedad Argentina para el Estudio de los Mamíferos, Mendoza, Argentina.
- DIAZ, G. B., R. A. OJEDA, M. H. GALLARDO, AND S. M. GIANNONI. 2000. Tympanoctomys barrerae. Mammalian Species 646:1–4.
- DIAZ, G. B., R. A. OJEDA, AND E. L. REZENDE. 2006. Renal morphology, phylogenetic history and desert adaptation of South American hystricognath rodents. Functional Ecology 20:609–620.
- EBENSPERGER, L. A., R. SOBRERO, V. CAMPOS, AND S. M. GIANNONI. 2008. Activity, range areas, and nesting patterns in the viscacha rat, *Octomys mimax*. Journal of Arid Environments 72:1174–1183.
- ELLERMAN, J. R. 1940. The families and genera of living rodents. British Museum of Natural History, London, United Kingdom.
- GALLARDO, M. H. 1997. A saltation model of karyotypic evolution in the Octodontoidea (Mammalia, Rodentia). Pp. 347–365 in Chromosomes today (H. Henríquez-Gil, J. S. Parker, and M. J. Puertas, eds.), Vol. 12. Chapman & Hall, London, United Kingdom.
- Gallardo, M. H., J. W. Bickham, R. L. Honeycutt, R. A. Ojeda, and N. Köhler. 1999. Discovery of tetraploidy in a mammal. Nature 401:341.
- Gallardo, M. H., J. W. Bickham, G. Kausel, N. Köhler, and R. L. Honeycutt. 2003. Gradual and quantum genome size shifts in the hystricognath rodents. Journal of Evolutionary Biology 16: 163–169.
- Gallardo, M. H., et al. 2004. Whole-genome duplications in South American desert rodents (Octodontidae). Biological Journal of the Linnean Society 82:443–451.
- Gallardo, M. H., and J. A. W. Kirsch. 2001. Molecular relationships among Octodontidae (Mammalia: Rodentia: Caviomorpha). Journal of Mammalian Evolution 8:73–89.
- Gallardo, M. H., R. A. Ojeda, C. A. González, and C. A. Ríos. 2007. The Octodontidae revisited. Pp. 695–719 in The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson (D. A. Kelt, E. P. Lessa, J. Salazar-Bravo, and J. L. Patton, eds.). University of California Publications in Zoology 134:1–988.

- George, W. 1986. The thermal niche: desert sand and desert rock. Journal of Arid Environments 10:213–224.
- Giannoni, S. M., C. E. Borghi, and R. A. Ojeda. 2000. Feeding behaviour of *Tympanoctomys barrerae*, a rodent specialized in consuming *Atriplex* leaves. Journal of Arid Environments 46: 117–121.
- Honacki, J. H., K. E. Kinman, and J. W. Koeppl (eds). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc., and the Association of Systematics Collections, Lawrence, Kansas.
- Honeycutt, R. L., D. L. Rowe, and M. H. Gallardo. 2003. Molecular systematics of the South American caviomorph rodents: relationships among species and genera in the family Octodontidae. Molecular Phylogenetics and Evolution 26:476–489.
- International Union for Conservation of Nature and Natural Resources. 2009. The IUCN Red list of threatened species. www.iucnredlist.org, accessed 6 January 2010.
- KÖHLER, N., M. H. GALLARDO, L. C. CONTRERAS, AND J. C. TORRES-MURA. 2000. Allozymic variation and systematic relationships of the Octodontidae and allied taxa (Mammalia, Rodentia). Journal of Zoology (London) 252:243–250.
- LAWRENCE, B. 1941. A new species of *Octomys* from Argentina. Proceedings of the New England Zoological Club 18:43–46.
- MARES, M. A. 1973. Desert rodent ecology: review for the origin and structure of ecosystems convergent evolution research program. Acta Zoologica Lilloana 30:207–225.
- MARES, M. A. 1975. South American mammal zoogeography: evolution in desert rodents (physiological ecology/multivariate analyses). Proceedings of the National Academy of Sciences 72: 1702–1706.
- MARES, M. A. 1976. Convergent evolution of desert rodents: multivariate analysis and zoogeographic implications. Paleobiology 2: 39–64.
- MARES, M. A. 1980. Convergent evolution among desert rodents: a global perspective. Bulletin of Carnegie Museum of Natural History 16:1–51.
- MARES, M. A., J. K. Braun, R. M. Barquez, and M. M. Diaz. 2000. Two new genera and species of halophytic desert mammals from isolated salt flats in Argentina. Occasional Papers, Museum of Texas Tech University 203:1–27.
- MARES, M. A., AND T. E. LACHER, JR. 1987. Ecological, morphological, and behavioral convergence in rock-dwelling mammals. Current Mammalogy 1:307–348.
- MARES, M. A., J. MORELLO, AND G. GOLDSTEIN. 1985. The Monte Desert and other subtropical semi-arid biomes of Argentina, with comments on their relation to North American arid areas. Pp. 203–237 in Hot deserts and arid shrublands (M. Evenari, ed.). Elsevier Publishers, Amsterdam, The Netherlands.
- MARES, M. A., AND R. A. OJEDA. 1982. Patterns of diversity and adaptation in South American hystricognath rodents. Pp. 393–432 in Mammalian biology in South America (M. A. Mares and H. H. Genoways, eds.). Special Publication 6, Pymatuning Laboratory of Ecology, Linesville, Pennsylvania.
- Mares, M. A., R. A. Ojeda, C. E. Borghi, S. M. Giannoni, G. B. Diaz, and J. K. Braun. 1997. How desert rodents overcome halophytic plant defenses. BioScience 47:699–704.
- MARQUEZ, J. 1999. Las áreas protegidas de la Provincia de San Juan. Multequina 8:1-10.
- MÁRQUEZ, J., E. MARTÍNEZ CARRETERO, A. DALMASSO, G. PASTRÁN, AND S. ORTIZ. 2005. Las áreas protegidas de la provincia de San Juan (Argentina) II. La vegetación del Parque Provincial de Ischigualasto. Multequina. Latin American Journal of Natural Resources 14:1–27.
- Morello, J. 1958. La provincia fitogeográfica del Monte. Opera Lilloana 2:1–155.
- Novak, R. 1999. Walker's mammals of the world. 6th ed. Johns Hopkins University Press, Baltimore, Maryland.
- NUTT, K. J. 2005. Philopatry of both sexes leads to the formation of multimale, mutifemale groups in *Ctenodactylus gundi* (Rodentia: Ctenodactylidae). Journal of Mammalogy 86:961–968.
- OJEDA, R. A., C. E. BORGHI, G. B. DIAZ, S. M. GIANNONI, M. A. MARES, AND J. K. BRAUN. 1999. Evolutionary convergence of the highly

- adapted desert rodent *Tympanoctomys barrerae* (Octodontidae). Journal of Arid Environments 41:443–452.
- OJEDA, R. A., C. M. CAMPOS, J. M. GONNET, C. E. BORGHI, AND V. ROIG. 1998. The MaB Reserve of Nacuñán, Argentina: its role in understanding the Monte Desert biome. Journal of Arid Environments 39:299–313.
- OJEDA, R. A., AND G. B. DIAZ. 1997. La categorización de los mamíferos de Argentina. Pp. 73–154 in Libro rojo de mamíferos y aves amenazados de Argentina (J. G. Fernandez, R. A. Ojeda, R. Fraga, G. B. Diaz, and R. J. Baigún, eds.). Administración de Parques Nacionales, Capital Federal, Buenos Aires, Argentina.
- OJEDA, R. A., J. M. GONNET, C. E. BORGHI, S. M. GIANNONI, C. M. CAMPOS, AND G. B. DIAZ. 1996. Ecological observations of the red vizcacha rat, *Tympanoctomys barrerae* in desert habitats of Argentina. Mastozoología Neotropical 3:183–191.
- OJEDA, R. A., AND S. TABENI. 2009. The mammals of the Monte Desert revisited. Journal of Arid Environments 2:173–181.
- OLIVARES, A. I., D. H. VERZI, AND A. I. VASALLO. 2004. Masticatory morphological diversity and chewing modes in South American caviomorph rodents (family Octodontidae). Journal of Zoology (London) 263:167–177.
- OPAZO, J. C. 2005. A molecular timescale for caviomorph rodents (Mammalia, Hystricognathi). Molecular Phylogenetics and Evolution 37:932–937.
- Orlog, C. C., and M. M. Lucero. 1981. Guía de los mamíferos argentinos. Ministerio de Educación, Fundación Miguel Lillo, Buenos Aires, Argentina.
- Oyarce, C. 2005. Usos de recursos alimentarios por *Octomys mimax* en el Parque Provincial Ischigualasto (San Juan, Argentina). B.A. thesis, Instituto San Pedro Nolasco, Mendoza y Universidad Aconcagua, Mendoza, Argentina.
- RANDALL, J. A., K. ROGOVIN, P. G. PARKER, AND J. A. EIMES. 2005. Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. Behavioral Ecology 16:961–973.
- RECA, A., C. ÚBEDA, AND D. GRIGERA. 1996. Prioridades de conservación de los mamíferos de Argentina. Mastozoología Neotropical 3:87–117.
- REDFORD, K. H., AND J. F. EISENBERG. 1992. Mammals of the Neotropics: the Southern Cone. University of Chicago Press, Chicago, Illinois.
- Reig, O. A. 1970. Ecological notes on the fossorial octodontid rodent Spalacopus cyanus (Molina). Journal of Mammalogy 51:592–601.
- Reig, O. A. 1986. Diversity patterns and differentiation of high Andean rodents. Pp. 404–439 in High altitude tropical biogeography (F.

- Vuilleumier and M. Monasterio, eds.). Oxford University Press, Oxford, United Kingdom.
- Spotorno, A. E. 1979. Contrastación de la macrosistemática de roedores caviomorfos por análisis de la morfología reproductiva masculina. Archivos de Biología y Medicina Experimentales (Chile) 12:97–106.
- Thomas, O. 1920. On mammals from near Tinogasta, Catamarca.
  Annals and Magazine of Natural History, Series 9 6:117–
  119
- Thomas, O. 1921. On mammals from the Province of San Juan, Western Argentina. Annals and Magazine of Natural History, Series 9 8:214–221.
- Trainor, C., A. Fisher, J. Woinarski, and S. Churchill. 2000. Multiscale patterns of habitat use by the carpentarian rock-rat (*Zyzomys palatalis*) and the common rock-rat (*Z. argurus*). Wildlife Research 27:319–332.
- VASSALLO, A. I., AND D. H. VERZI. 2001. Patrones craneanos y modalidades de masticación en roedores caviomorfos (Rodentia, Caviomorpha). Boletín de la Sociedad de Biología de Concepción (Chile) 72:145–151.
- Verzi, D. H. 2001. Phylogenetic position of *Abalosia* and the evolution of the extant Octodontinae (Rodentia, Caviomorpha, Octodontidae). Acta Theriologica 46:243–268.
- Verzi, D. H., and C. A. Quintana. 2005. The caviomorph rodents from the San Andre's Formation, east-central Argentina, and global late Pliocene climatic change. Palaeogeography, Palaeoclimatology, Palaeoecology 219:303–320.
- Wells, P. V. 1976. Macrofossil analysis of woodrat (*Neotoma*) middens as a key to the Quaternary vegetational history of arid America. Quaternary Research 6:223–248.
- WILKINS, K. T., AND L. L. CUNNINGHAM. 1993. Relationship of cranial and dental features to direction of mastication in tuco-tucos (Rodentia: *Ctenomys*). Journal of Mammalogy 74:383–390.
- WOODS, C. A., AND C. W. KILPATRICK. 2005. Infraorder Hystricognathi
  Brandt, 1855. Pp. 1538–1600 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.), 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- YEPES, J. 1930. Los roedores octodóntidos con distribución en la zona cordillerana de Chile y Argentina. Revista Chilena de Historia Natural 34:321–331.
- YEPES, J. 1942. Zoogeografía de los roedores octodóntidos de Argentina y descripción de un género nuevo. Revista Argentina de Zoogeografía 2:69–81.

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